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ON

THE FORMS AND STRUCTURE

OF

FERN-STEMS.

BY

GEORGE OGILVIE, M.D.,
LECTURER ON THE INSTITUTES OF MEDICINE IN MARISCHAL COLLEGE
AND UNIVERSITY, ABERDEEN.

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FORMS AND STRUCTURE OF FERN-STEMS.

On the Vegetative Axis of Ferns.—For the following observations the author makes no further claim to originality than that they were suggested to him by researches which he was led to undertake from finding the subject scarcely noticed at all in our common botanical works.

External Characters of Fern-stems.

By the corm or vegetative axis of Ferns, it is hardly necessary to mention, is meant that part which, in our indigenous species is commonly termed the *root*, as being more or less buried in the soil, though it does not differ essentially from the arborescent stem of the Tree-ferns of tropical and southern latitudes. Even in our British species, however, the corm or vegetative axis presents considerable diversity of form. The author has to regret that his opportunities of investigating the varieties of this organ have been so limited. He has been restricted, not only to our indigenous species, but, with few exceptions, to those growing in his own neighbourhood; for, though specimens of fern-fronds are readily enough to be had in exchange, few collectors preserve the rhizomes. From the examination, however, of such species as he has been able to procure, he believes that the corms of our British Ferns—if not of the tribe generally—may be reduced to the three forms of a stoloniferous rhizome, and a caudex, simple or branched.

These varieties depend on the relations and proportionate development of the principal structural elements—the proper axis, the rootlets, and the fronds, whose bases remain permanently attached to the stem after the leaf-like portions have withered and decayed away. Organs corresponding to these enter into the constitution of all the higher plants. In the larger forms of vegetation, they are clearly marked off from each other by a wide local separation, the radical fibres coming off

from one extremity of the stem, and the leaves from the other; but this arrangement is not an essential of the vegetable organization; for in various subterranean and creeping stems, such as those of the rose and the iris, the strawberry and many grasses, we have both rootlets and leafy shoots coming off side by side from a greater or less extent of the vegetative axis; and even where this assumes an arborescent character, such intermixture, though less frequent and less complete, is still an arrangement of occasional occurrence, as in the Banyan and other species of *Ficus*, *Pandanus*, *Dracæna*, &c. All these variations we have represented in Ferns. In Tree-ferns, as in arborescent forms of other types of vegetation, we have the length of the stem interposed between the rootlets and the bases of the fronds; and though generally, when the plant attains some height, adventitious roots are emitted from the sides of the stem, still they spring from its lower part, and are separated from the growing leaves by a very considerable interval. But in our indigenous species the stems are all more or less of the kind termed *rhizomes* by botanists, and emit rootlets and leaf-stalks side by side along their whole extent, or nearly so; and, as has just been remarked, it is to diversities in their disposition and proportionate development that the variations in the form of the stem are in great measure due.

In the first or stoloniferous variety, the axis is long, slender, and much branched, its subdivisions running horizontally along or just under the surface of the ground, and sending off from below numerous black wiry rootlets, and from the upper aspect the scattered petioles of the fronds. The extremities of the rhizome are scaly, the petioles smooth and naked. When a root of this kind is dissected out of the soil—an operation involving no small expenditure of time and trouble, from its tortuous and brittle character—we can readily distinguish the formations of successive years. At the growing points of the stolons we have the petioles quite fresh, and still bearing leaves; behind these, we have the bases of the last and former years' fronds in different stages of decay; and lastly, only the creeping stem itself, and this, as we trace it backwards, in a continually increasing state of decay, which finally makes it impossible to follow it any further. By this disappearance of the common connecting portion of the rhizome, the later branches assume the position of independent plants, and the forest of fronds covering the turf may be compared to the vigorously vegetating leaf-shoots of a subterranean shrub whose trunks have already mouldered away.

Roots of this description occur in all our Polypodies (Pl. VIII. figs. 1, 2), in the Bracken, in *Hymenophyllum*, and probably also in *Adiantum*, *Trichomanes*, and in *Lastrea Thelypteris*.

The common Polypody, however, has one peculiarity, in which it stands alone among our indigenous Ferns,—that its petioles break off by articulations, so that the older portions of the stem do not bear the stumps of former leaf-stalks, but only cicatrices marking their insertions.

To this variety the form described as the simple caudex stands in the most marked contrast. Its characteristic features are the number and spiral arrangement of the petioles of the leaves. At its growing extremity these form one of the graceful circles of bright green foliage, which are so pleasing a feature in the vegetation of our larger Ferns. The axis itself is sometimes of considerable thickness, but its real dimensions are not distinguishable at first sight, from its being so completely ensheathed in the persistent bases of the decayed fronds of former years. Its direction of growth varies from horizontal to vertical (Pl. X. figs. 7, 8). In the former case, it creeps along or just under the surface of the ground, and forms a more or less considerable angle with the terminal crown of fronds, the axis of which is always vertical, owing to a corresponding curvature of the petioles at their points of origin. In cases, again, where the axis of the stem approaches the vertical, as in some foreign species of *Blechnum, Struthiopteris*, &c., it gradually rises above the ground in the course of growth, and assumes on a small scale the features of the arborescent form, the terminal circle of leaves corresponding with that elegant palm-like crown of foliage which is so prominent a characteristic of the Tree-ferns. The correspondence between such a caudex and the corm of a Tree-fern is brought out more clearly by cutting off all the bases of the old fronds at their points of insertion, when we obtain a nearly cylindrical stem, marked with rhomboidal scars, answering to those which, in most arborescent species, indicate the points of insertion of fallen petioles (Pl. X. fig. 9).

In this operation we have to clear away numerous radical fibres, as well as the petioles of old fronds, for the rootlets are equally abundant in this as in the former or stoloniferous variety, though, from the closeness of the leaf-stalks, between whose insertions they originate, they form but a secondary feature, except at the lower parts of the corm, where the decay of the petioles allows them greater prominence. This form of stem would probably be better termed a right or straight than a simple caudex, for it generally bears *lateral* buds, giving rise to secondary rhizomes (Pl. X. fig. 10). Sometimes these appear to be deciduous, or to be pushed off by the growth of the petioles. In any case, they will of course become independent plants when the decay of the lower extremity of the caudex reaches their points of origin.

As examples of this form of caudex may be mentioned *Lastrea Filix mas, L. dilatata, L. cristata, Polystichum aculeatum,* and *P. Lonchitis.*

The other form of caudex is intermediate between this last variety and the stoloniferous rhizome first described; for the axis branches so repeatedly in a dichotomous manner, by the duplication of its terminal buds, that, when dissected out, it has somewhat the character of the stoloniferous rhizome; but in its natural state it is so thickly set both with foot-stalks and rootlets, that nothing is to be distinguished but a mass of tangled roots, more or less tufted above and densely fibrous below.

A caudex of one kind or other occurs in all our larger Ferns except *Pteris aquilina,* and in the majority it appears to be branched. So at least it is in *Allosurus crispus, Blechnum boreale, Osmunda regalis, Lastrea Oreopteris,* and in *Filix fœmina* and the genus *Asplenium* generally. (Pl. VIII. fig. 3; IX. figs. 4, 5, 6.)

It is doubtful if the branched caudex ever becomes arborescent as a normal occurrence*. Branched Tree-ferns are certainly met with, but rather, it would seem, as an occasional abnormality than as a regular form.

Among our native Ferns, *Ophioglossum* and *Botrychium* are remarkable for their vernation being straight, not circinate, as in the rest of the group, and the last-mentioned species also for the edges of the solitary petiole cohering, so as to embrace the point of the axis and form a cavity which lodges the embryo of the next year's frond; within *its* petiole the rudiments of the frond of the succeeding year may in like manner be detected. The stem itself may probably be considered a modification of the simple caudex.

Among the Fern-allies of our flora, the stoloniferous is the most common form of stem. In Equisetaceæ it is subterranean, like that of the Ferns; but in *Pilularia* and *Lycopodium* it creeps along the surface of the ground. In the larger species of *Lycopodium* the successive stages of annual growth, and the separation of the shoots as independent plants by the gradual decay of the older portion of the stem, are more clearly brought out than even in the stoloniferous roots of Ferns. In *Isoëtes* we have a peculiarly modified form of the simple caudex.

Internal Structure of Fern-stems.

The next point to be noticed is the internal structure of the vegetative axis of the Fern, principally as it affects the disposi-

* An analogical argument in favour of this may be drawn from Palm-stems, which are normally simple from the development of a single terminal bud, but which are branched in a few species, as *Phœnix,* or form lateral buds, as in *Areca, Caryota,* and *Chamærops.*

tion of the fibro-vascular bundles. Woody fibre and vessels (which, except in a few degraded species, are a universal characteristic of phanerogamic plants) occur, it is well known, only in the higher forms of cryptogamic vegetation—the Ferns and allied orders,—and even there but sparingly and with some remarkable peculiarities both in their minute structure and their general disposition. The most observable structural characters are the dark colour of the woody or hard tissue, and the large size, angular section, and scalariform markings on the ducts. In the disposition, too, of the fibro-vascular tissue, the stems of Ferns present some remarkable peculiarities, quite as distinct as those characteristic of the better-known divisions of the so-called Endogenous and Exogenous stems. These differences do not so much affect the original constitution of the stem as the mode in which the successive annual increments are applied to the primary axis. In vascular shoots of the first year, whether Dicotyledonous, Monocotyledonous, or Cryptogamic, there is comparatively little difference. In each we have a single circle of fibro-vascular bundles imbedded in the general cellular tissue of the stem; but when the new bundles of subsequent years come to be added, we find the characteristic differences clearly brought out. Thus the peculiarities of the Exogenous stem depend on the addition to the exterior of the wood and interior of the liber of former years, of annual layers, forming in section concentric circles of ligneous and cortical tissue. Hence the accretions to the wood of a Dicotyledonous stem have been represented by a number of cones of continually increasing dimensions placed one over the other, and slightly truncated at the top. In horizontal sections the wood of such a stem presents a series of concentric rings, which represent the bases of the cones, interrupted by radiating bands of muriform tissue, which are the outward continuations of the cellular interspaces between the bundles of the original circle, and represent the small residue of the cellular element of the stem left after the abundant development of fibro-vascular tissue characteristic of the Dicotyledonous organization. In a tangental section, these same bands are seen cut across, and may be observed to occupy the meshes left by the interlacement of the longitudinal fibro-vascular bundles. Though the formation of wood in Dicotyledonous plants is spoken of as being on the exterior, and has hence given rise to the stem being termed Exogenous, still it is to be remembered that at the growing points the fasciculi do in fact pass from the petioles of the leaves into the interior of the stem, and only gain that position which characterizes the rest of their course by curving outwards again to apply themselves to the exterior of those of older formation.

In the Monocotyledonous stem, again, the fibro-vascular fasciculi, though they tend at last in the same way to place themselves on the outside of those of older development, lose themselves here, by the dispersion and occasional anastomosis of their elements, in what has been termed the fibrous layer of the stem, and do not descend any way on the exterior, or form any new continuous envelope like an annual layer of Exogenous wood. Hence, should we wish to represent the increments of a Monocotyledonous stem by a series of superposed truncated cones, we must make them, not, as in Dicotyledons, of continually increasing dimensions, so that the outer shall completely envelope the inner, but we must make them all of the same size, so that the series as a whole may have, not a conical but a cylindrical outline, the outer cones being borne up by those within and below them, whose bases they can no longer cover. They are also more truncated or more open at the top, from the larger size of the cellular core of the terminal bud. Such a stem, on horizontal section, is described as presenting three regions:—1st. A central, which in some respects corresponds to the pith of a Dicotyledon, but which contains imbedded in the cellular tissue the ends of numerous fibro-vascular bundles, divided in their descending but at the same time outward-bound course through the interior of the stem. 2ndly. A cortical zone, also of cellular tissue, differing from the bark of a Dicotyledon in not being generally separable from the stem, and in rarely containing any fibrous tissue. 3rdly. Intermediate between the central and cortical regions, a ring of densely-matted fibrous tissue, formed by the anastomosis of the lower and outer ends of the fibro-vascular bundles.

In the stems of Ferns, the fibro-vascular element is but very sparingly developed in proportion to the cellular, and the disposition of the fasciculi assumes in consequence a different appearance from that in either of the higher groups; the vascular bundles are well developed in the petioles of the fronds, but they enter no further into the structure of the stem than simlpy to effect a union with those derived from the fronds of former years. They have no downward course in the stem; the arched fibres in the interior, characteristic of the Endogenous stem, and the annual layers of descending woody tissue on the exterior (so conspicuous a feature in that of Exogens), are alike wanting; for the fasciculi, immediately on entering the stem, branch out and anastomose with those derived from former petioles, forming a very beautiful reticulated cylinder near the exterior, analogous evidently to the "fibrous layer" of the Monocotyledonous stem, but presenting, instead of the dense fibrous interlacement of the latter, a network of thick cords of scalari-

form tissue, ensheathed in a layer of brownish pleurenchyma, and separated by large open meshes, through which the cellular tissues of the central and cortical regions are freely continuous with each other (Pl. X. fig. 11). The pile of superposed truncated cones, diagrammatically representing the Exogenous stem —already cut down all to one length, and more opened at the top to adapt them to the Endogenous type—must now be reduced to a series of simple rings placed one upon another.

On a longitudinal section along the axis, a fern-stem presents a uniform expanse of cellular tissue, marked only by an interrupted line near each margin, indicating the position of the fibro-vascular bundles of the reticulated cylinder, the interrupted spaces answering to the meshes of the network (fig. 10). On a horizontal section we have a corresponding interrupted circle formed by the cut extremities of the fibro-vascular anastomosing cords (fig. 12). This circle divides the section into a large central and a smaller cortical region, both composed of cellular tissue, as in the Monocotyledonous stem, but without the descending fibres which form so conspicuous a feature in the interior of the latter. In a certain point of view, these regions correspond to the pith and cellular bark of a young Dicotyledonous stem, in which the cellular tissue has not yet been displaced by the fibro-vascular element; and the interspaces of the reticulations may be held to represent the medullary rays. Indeed, in all the fibrous tissues of Dicotyledonous plants a tendency may be observed to such an interlacement about the medullary rays: it is quite obvious to the naked eye in the bast-fibres of the Lime and many other trees; it has been noticed in the medullary sheath of Coniferæ, and it may be seen with great distinctness under the microscope, in tangental sections of mahogany and other hard woods.

The stems of Tree-ferns are said to be generally hollow, but the character is not an essential one. Fistulous stems are well known to occur both in Endogenous and Exogenous plants*, and probably always depend on the shrinking of a lax cellular tissue originally filling the space. Hollow stems are not described as occurring in any of our indigenous Ferns, but it may generally be observed that in the decayed portions of a rhizome the central cellular tissue is the first to disappear.

The most elegant and instructive preparation of a fern-stem is made by dissecting off the outer cortical layer so as to expose the reticulated structure of the fibro-vascular cylinder. Two sets of fasciculi will then be seen to be connected with its exterior,

* In Endogens, the Cocoa-nut and other Palms and most grasses, in Exogens, many Umbelliferæ, Compositæ, and Labiatæ furnish instances of this.

—the one derived, as already noticed, from the bases of the petioles, the other continuous with the rootlets.

The rootlets of Ferns are emitted in succession from below upwards, in proportion as they are required for the nutriment and mechanical support of the plant. The latter is probably the main use of the so-called adventitious roots, which are sent forth in such numbers from the lower part of the stem in some Tree-ferns as to cause a remarkable increase in the diameter of the base. The nutriment introduced by the roots must be carried up by imbibition through the cellular matter of the stem, or through the fibro-vascular network derived from the bases of petioles long since decayed. In any case, it is evident that, whatever may be alleged in favour of regarding a Dicotyledonous tree as a mere aggregation of slender stem-bound phytons, whose leaf-bearing shoots form its present foliage, while their downward extremities are continuous with the active spongioles of the roots, such a view cannot be held tenable in the case of Ferns. In this group at least, and probably also in Monocotyledons, we must admit two fundamentally distinct foci of vital action—the leaf-bud and the rootlet,—the former originating from the upper extremity of the stem, the latter connecting itself with its lower portions. In neither of these forms of vegetation can the rootlets be regarded (as some would regard them in Dicotyledons) merely as the onward continuation of fasciculi sent down from the leaves, for the bundles of the leaf-stalks descend, in Monocotyledonous plants, but a small way along the stem, and in Ferns not at all; while, in arborescent species, the radicles are emitted only from the inferior parts, far below the point reached by the former.

There is every reason to believe that the emission of the rootlets is a purely local action, and Prof. Henfrey's description of it in Monocotyledons seems to apply also in Ferns*. According to this author, the first rudiment of the rootlet is a funnel-shaped circle of fasciculi in the cortical region at the base of the stem, which, on the one hand, implant themselves upon the fibrous layer within, and, on the other, converge to form the central axis of the rootlet, and force their way outwards through the tissue of the cortical zone in which they were developed. Without venturing to say how far this local formation of rootlets may occur also in Dicotyledons, it may be remarked that in all forms of radical fibres the vascular bundles have an arrangement different from that in the stem, and such as would follow from this mode of formation,—the fasciculi lying in the axis of the rootlet, to the exclusion of the pith or cellular core which occupies the central region in all the upward shoots. It may be

* Ann. Nat. Hist. i. 187.

observed also, that, even in Dicotyledons, a certain vegetative independence is indicated in the origin of rootlets, from the local application of moisture so fostering their production as to cause their development even from abnormal parts.

It does not appear that the assumption of two distinct developments of vegetative power in the guise of leaf-buds and rootlets—or, as they might be termed, *phyllophytons* and *rhizophytons,*—is at all opposed to the analogy of other forms of organization; for we observe a corresponding diversity of individualized organs in various compound animals, as, for instance, in the alimentary, generative, and protective appendages of Hydractinia, the polypes and avicularia of the Polyzoa, and the cirrhi and ovarian capsules of the Physograda,—parts which may certainly be *assumed* to be mere modifications of a common original form, but between which it would not be easy to point out much community of structure in proof of such co-relative derivation.

There still remains for consideration the arrangement of the dark-coloured tracts commonly regarded as of the nature of woody tissue; but for the present it may suffice to notice the great diversity which prevails in different species in the disposition of these fasciculi. Thus, in *Osmunda* we have an accumulation of dark tissue on the exterior of the caudex; in *Blechnum boreale,* again, it occupies the interior; in *Pteris aquilina* it forms broad bands interposed between an outer and inner layer of vascular tissue; while in *Filix mas* it exists only as a thin stratum ensheathing the latter; in *Lastræa dilatata* it occurs in isolated masses in the cellular core of the rhizome.

The author may remark, in conclusion, that but a few days ago his attention was called by a friend to an incidental notice —the only one he has yet met with—of the fibro-vascular system of Ferns, in a paper on Sigillaria in the 'Edinburgh Philosophical Journal' for 1844, by Mr. King of Newcastle, which, from its geological title, he had previously overlooked. Mr. King's remarks, so far as they go, will be found quite in accordance with the foregoing. He surmises that in Tree-ferns (owing to the greater development of the longitudinal fasciculi) the regular rhomboidal meshes may be reduced to long narrow slits. This is the more probable from an arrangement precisely of this kind obtaining in creeping rhizomes, such as those of the bracken. It is well known to botanists that there is a similar diversity in the extension of the medullary rays of Exogens: they are much larger, for instance, in the oak than in most other woods, and in the *Clematis* they reach the whole length of the internodes, so that, when they decay, the stem breaks up by the separation of its component woody wedges.

EXPLANATION OF PLATES.

Plate VIII.

Fig. 1. A portion of the branched and creeping rhizome of *Polypodium Phegopteris*, showing the fringe of wiry rootlets and the persistent bases of old leaf-stalks.

Fig. 2. The branched and creeping rhizome of *Polypodium vulgare.* It is more thickly set with rootlets than the last, and marked with the scars of fallen petioles.

Fig. 3. The dichotomous caudex of *Blechnum boreale,* with the axis exposed by cutting off, close to their origin, all the foot-stalks of former years' fronds.

Plate IX.

Fig. 4. The dichotomous caudex of a large bushy specimen of *Allosurus crispus,* stripped of the rootlets, the petioles of former years, and of most of the fronds.

Fig. 5. The dichotomous caudex of *Asplenium Filix fœmina,* exposed by a section along the axis of its several branches, to show the connexion of the bases of the leaf-stalks of successive years with the core of the stem.

Fig. 6. Another specimen of the same species, with the caudex stripped of its rootlets and petioles, the scars with which it is marked indicating their points of attachment. Of these there must be considerably more than a thousand: the plant had certainly upwards of a hundred fresh fronds when dug up.

Plate X.

[Illustrations of the rhizome of *Lastrea Filix mas.*]

Fig. 7. A caudex which has been forced into an upright line of growth.

Fig. 8. Another specimen, showing the usual horizontal direction of growth, the terminal bud forming an angle with the rhizome.

Both these specimens are in their natural state.

Fig. 9. Tessellated appearance of the surface of the caudex when the petioles are cut off close to their origin. The dots indicate the cut ends of the vascular bundles going to the fronds.

Fig. 10. Perpendicular section of an upright caudex, showing the interrupted line on each side of the axis, where the reticulated fibro-vascular cylinder has been divided by the section. The figure shows also the connexion of the bases of the petioles, and a lateral bud arising from one of them.

Fig. 11. A portion of a preparation showing the netted fibro-vascular cylinder of the caudex, removed entire by careful dissection from the cellular matrix. The further side of the cylinder is imperfectly shown, from having been out of focus in the photograph. The secondary fasciculi, proceeding to the leaf-stalks and rootlets, give the exterior a bristly appearance.

Fig. 12. A diagrammatic transverse section of the caudex. The interrupted circle represents the cut extremities of the fasciculi of the netted cylinder, and the scattered dots on its exterior those of the secondary fibro-vascular bundles of the petioles and rootlets.

[The above figures are mostly from photographs of the original specimens (now in the Museum of the Royal Botanic Garden, Edinburgh) by Mr. Andrew Adams of Aberdeen.]

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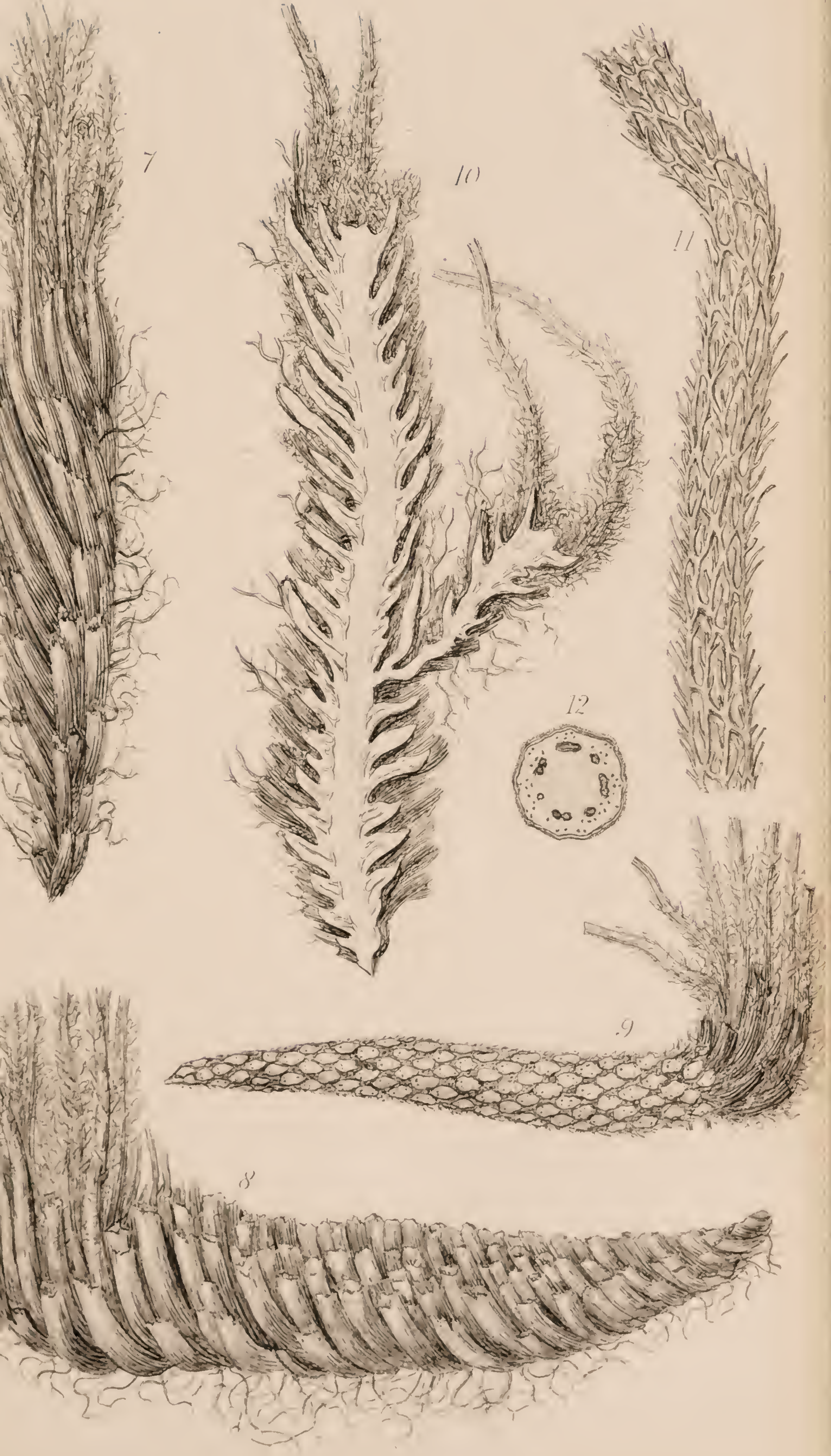
J. D. C. Sowerby



J. De C. Sowerby

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